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Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the southern Appalachians

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Abstract

Small canopy openings often alter understory microclimate, leading to changes in forest structure and composition. It is generally accepted that physical changes in the understory (i.e., microclimatic) due to canopy removal drive changes in basic forest processes, particularly seedling recruitment which is intrinsically linked to soil moisture availability, light and, to a lesser extent, temperature. We examined the impact of small canopy gaps of the type (snags) and size ($\sim$300 m^2) most frequently observed in the southern Appalachians on the understory microclimate. We created artificial canopy gaps at two elevations (a.m.s.l.) by girdling trees in areas with and without a *Rhododendron maximum* L. (rosebay rhododendron) understory. Soil and air temperature ($^\circ$C), photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}), and volumetric soil water content (%WC) in the upper 15 cm of soil were measured along transects generally running north to south through each gap. Overall, PAR was substantially less in rhododendron gaps than in non-rhododendron gaps. We found a slight increase in PAR in non-rhododendron gaps during spring and summer compared to controls. Very little seasonal variation in PAR was observed in rhododendron gaps compared with non-rhododendron gaps. In general, %WC in rhododendron gaps was lower than in non-rhododendron gaps and less variable. We also found a gap response in incident PAR during the spring and summer seasons. There was no significant effect of gap creation on %WC, nor were there site (elevation) differences or effects due to the presence of rhododendron. Further, there was no significant gap effect on mean, maximum, or minimum soil and air temperature; however, there were significant effects from the presence of rhododendron and between sites for PAR and soil and air temperature during certain seasons of the year. Although there is some certainty about measurable responses in key microclimatic variables in rhododendron and non-rhododendron gaps found in this study, we could not be certain if responses represent a significant enough departure from values in undisturbed conditions to elicit a tree recruitment response. Our results indicate that for openings of the size examined here, topography and evergreen understory are the primary determinants of spatial and temporal heterogeneity in understory microclimate.
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1. Introduction

Small openings in forest canopies are common and important sources of spatial heterogeneity in forest ecosystems. These 'canopy gaps' form as a result of

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canopy level disturbances caused by the death of an individual tree or a small cluster of trees. Such tree mortality can result from a variety of causes including: root fungi, such as *Armillaria mellea* Vahl ex Fr. (Shaw and Kile, 1991; Lundquist, 1993), cambially active fungi, such as the chestnut blight (*Cryphonectria parasitica* [Murr.] Barr) (Anagnostakis and Hillman, 1992) and dogwood anthracnose (*Discula destructiva*) (Daughtrey and Hibben, 1983), or allogenic influences such as high winds (Foster, 1988; Peterson and Pickett, 1991; Myers and van Lear, 1997). However, catastrophic events, sometimes referred to in the literature as LIDS (large, infrequent disturbances) (Foster et al., 1998), usually result in large areas of disturbance. Forest responses to LIDS are very different, both temporally and spatially from responses to small canopy gaps.

The current paradigm of forest dynamics emphasizes the role of small canopy gaps in the maintenance of forest diversity. Denslow (1980) asserts that forest communities in which large-scale disturbances are rare are characterized by many tree species that reach the canopy through small gaps and few that depend on large openings for establishment. Implicit in Denslow's hypothesis is that for all sizes of canopy openings there is a predictable response. For small gaps, however, recruitment as a response is, at best, difficult to predict and varies within and among forest types. For example, Canham et al. (1990) have shown that for a given gap size, gap influence diminishes with increasing latitude and increasing tree height to the extent that at the extremes, gap influence with the exception of inputs (e.g., atmospheric deposition, precipitation, woody and non-woody debris) is essentially non-existent. Small openings in the forest canopy, no matter how common, may not be the key drivers of forest processes they are assumed to be.

In general, disturbances within forests influence the availability of resources such as light, water, and nutrients (Marks, 1974; Bormann and Likens, 1979; Carlson and Groot, 1997) which are critical for seedling establishment and growth. The optimum level of resource availability necessarily varies among species where wide differences in understory tolerance (i.e., drought, shade, competition, allelopaths, etc.) exist. However, increases in the most limiting resources (e.g., light) can promote rapid re-growth of successional vegetation (Uhl et al., 1988), but do not always

result in new recruits (Ehrenfeld, 1980). Observed increases in resource availability are most pronounced in large patches where the influence of surrounding vegetation is minimized (Marks, 1974). For example, Phillips and Shure (1990) found that large versus small openings cause the greatest change in microclimatic conditions in southern Appalachian forests. In addition, microtopographic variation due to disturbance results in within-gap spatial heterogeneity. For example, Clinton and Baker (2000) found that when pits and mounds are present within large or small gaps, factors such as soil temperature, soil moisture, light levels, and total soil nitrogen vary considerably across pit and mound microsites. Petersen and Campbell (1993) found that woody and herbaceous seedling recruitment also varied among pit and mound microsites. Thus, natural microtopographic variation within and among patch types and sizes results in highly variable responses in key drivers of forest processes.

Rhododendron maximum L. (rosebay rhododendron), a sclerophylous, evergreen shrub, is an important understory component of forests in the southern Appalachian mountains (Monk et al., 1985), where rhododendron thickets cover an estimated 1.2 million hectares (Cox, 1981; Dobbs, 1998). Thickets have increased in extent over the past 100 years due to changes in forest composition and structure resulting from episodic disturbances and shifts in forest management (McGinty, 1972; Monk et al., 1985; Phillips and Murdy, 1985). It is not uncommon for rhododendron densities to exceed 5000 stems ha^{-1} (Clinton et al., 1994), and several studies have shown that high densities of rhododendron interfere with canopy seedling establishment (Monk et al., 1985; Clinton et al., 1994; Beckage et al., 2000). While the low light under rhododendron thickets is probably the primary factor affecting seedling establishment (Clinton et al., 1994), soil and forest floor properties such as reduced nutrient availability and increased litter and humus depth, could also be factors (Nilsen et al., 2001). Rhododendron may also contribute to lower nutrient availability as a result of the increased sequestration of nutrients in its evergreen leaves (Monk et al., 1985). This species has historically been confined to riparian areas and other mesic sites, and prefers deep, well-drained acid soils high in organic matter. However, there is some evidence to suggest that due to fire suppression and the absence of other cultural activities (i.e., mountain-land

grazing), rhododendron has moved beyond the mesic forest sites into sub-mesic understories (Dobbs, 1998). Because of the importance of rhododendron in regulating forest regeneration processes, its continued occupation of current sites and expansion into new sites may have a significant influence on forest regeneration in small canopy gaps.

The objectives of this study were to: (1) assess the effect of a prevailing gap size/type combination on understory microclimatic conditions, and to (2) assess the effects of elevation and of rhododendron on microclimatic responses.

2. Methods

2.1. Site description

This study was conducted at the Coweeta Hydrologic Laboratory (35°03'N, 83°25'W) as part of the National Science Foundation (NSF) Long-Term Ecological Research (LTER) program. Coweeta is located in the Blue Ridge physiographic province of the southern Appalachian mountains of western North Carolina (USA), and lies on the east side of the Nantahala range (Swank and Crossley, 1988). The 2100 ha basin where the laboratory is located ranges in elevation from 700 to 1600 m. Rainfall is generally abundant (~1900 mm) and evenly distributed through the year with less than 5% falling as snow or ice. Mean annual air temperature is 12.6 °C and ranges from an average of 6.7 °C in the dormant season to 18.5 °C in the growing season (Swift et al., 1988). The soils are primarily Ultisols (Typic and Humic Hapludults) and Inceptisols (Umbric and Typic Dystrochrepts and Typic Haplumbrepts) (Velbel, 1988).

The mixed-oak forest type (Day et al., 1988) is widely distributed over the basin. The most widespread and important canopy species is *Quercus prinus* L. (chestnut oak), and is most frequent at mid-elevations. *Q. rubra* L. (northern red oak) dominates at high elevations, while at low elevations *Q. alba* L. (white oak) and *Q. velutina* Lam. (black oak) are important. *Q. coccinea* Muenchh. (scarlet oak) dominates the xeric mixed-oak type as well as oak-pine forests on drier slopes and ridges at low- and mid-elevations. Other important overstory species include *Liriodendron tulipifera* L. (yellow poplar), *Acer rubrum* L. (red maple),

and *Carya* spp. (hickories). The understory has a discontinuous evergreen shrub layer made up of *Kalmia latifolia* L. (mountain laurel) on relatively dry sites and rhododendron on mesic sites. In these forest systems, mature rhododendron sub-canopies are typically 2–8 m above the forest floor and can attain densities exceeding 5000 stems ha^{-1}. All species nomenclature follows Little (1979).

3. Experimental design

3.1. Gap creation

We tried to mimic natural gap formation, basing gap type (e.g., standing dead snag versus windthrow) and size (250 m^2) on past studies of canopy gaps in the Coweeta Basin. Clinton et al. (1993), in a study of drought-induced canopy gaps, found that average gap size in the basin was approximately 250 m^2 and that 90% were of the standing dead snag type. We chose two sites at different elevations (approximately 810 and 1130 m) based on the availability of large areas with no evergreen understory juxtaposed with large areas with understories dominated by rhododendron. At each site, we artificially created six canopy gaps, three with rhododendron (R) and three without (non-rhododendron or NR) by girdling canopy dominants and smaller sub-canopy trees in the vicinity to achieve a roughly elliptically shaped gap area of approximately 300 m^2. We applied herbicide (Garlon®, Dupont, Inc.) to the wound of each girdled tree to ensure mortality. Gaps at the lower elevation had generally a north—northeast aspect, while the upper elevation site had aspects of north—northwest.

3.2. Gap microclimate

Transects 40 m in length were established within each canopy gap in an approximate north/south direction. Gap edge was approximately 10 m from gap center. Both ends of the transects were well outside the artificial gap and were used as controls. We installed thermocouples 1 m above the forest floor along the transects to measure air temperature and 10 cm below the surface of the forest floor to measure soil temperature. Air temperature thermocouples were shielded from direct solar radiation with pvc caps, and

all thermocouples were tinned with solder. Thermo-couples were installed at 2 m intervals for 8 m in both directions from gap center and within the experimental gap. We installed an additional pair of thermocouples 20 m from gap center at both ends of the transects. Data from each air and soil temperature thermocouple pair were collected simultaneously every 15 min and averaged and stored on an hourly basis using multiplexers and dataloggers (Campbell Scientific, Ogden, Utah). We installed Time Domain Reflectometry (TDR) rods to a depth of 15 cm (rooting zone) at each thermocouple location for periodic measurement of volumetric soil moisture content. Measurements were made approximately monthly throughout the growing season. Throughout the study period, the high elevation site received on average 18% more precipitation per year than the lower elevation site, and ranged from 14 to 21% more through the period.

Photosynthetically active radiation (PAR, 400–700 nm) was measured on cloudless days between the hours of 1030 and 1330 on approximate 2-week intervals using a sunfleck ceptometer (Decagon, Inc.) in the PAR function for estimates of quantum flux. We recorded the average of four measurements at 1 m above the forest floor for each location along the transects; measurements of full sun were made in open locations near each study site for calculations of percent full sun. The height of 1 m above the forest floor for PAR measurements is well within the 2–8 m high rhododendron subcanopy.

4. Statistical analysis

The experimental design consisted of a split plot where the whole plot factor consisted of a 2×2 factorial combination of elevation and vegetation. It is important to note that there is no true replication on elevation and any observed differences are taken to be due to site differences, which are in part due to elevation. Replication consisted of three plots at each elevation and vegetation combination, however, due to constraints related to plot to plot proximity, vegetation 1 (with rhododendron) had only one plot at each elevation. The split plot factor was the two gap treatments which were applied to each half of the vegetation treatment plots. The whole plot factors

of elevation and vegetation and the elevation $\times$ vegetation interaction were tested with F tests where the denominator was the plot (elevation vegetation) mean square. The split plot factor treatment and all of its two and three way interactions with elevation and vegetation were tested with F tests using the typical residual mean square as the denominator. We examined statistical differences using PROC GLM (SAS Institute Inc., 1985) for PAR, volumetric soil water content, and mean, maximum, and minimum soil and air temperature by season, where appropriate. Where significant differences were found for the whole or split plot factors, LSMEANS (SAS Institute Inc., 1985) was used to generate means for main effects. With the exception of temperature, response variables were log-transformed to satisfy the requirement for homogeneity of variances across treatments (gap or no-gap) and understory condition (rhododendron or non-rhododendron). Significant differences were evaluated at the $\alpha = 0.10$ level.

5. Results and discussion

5.1. Light environment (PAR)

Within gaps, light attenuation was substantially influenced by the presence of rhododendron (Fig. 1). Light patterns followed typical seasonal patterns for both understory conditions at both elevations but maxima were considerably lower in rhododendron gaps. In non-rhododendron gaps, seasonal means for PAR (Fig. 2) varied considerably and were substantially higher during the dormant season, approaching 1000 μmol m^{-2} s^{-1} during early spring in all years; in the rhododendron gaps maxima remained well below 500 μmol m^{-2} s^{-1}. Rhododendron gaps also showed substantially less seasonal variation, and throughout the year remained well below light levels observed in non-rhododendron gaps.

We separated light responses by season of year to show spatial patterns of light along the north/south transects (Fig. 2). Predictably, the magnitude and variation in light responses differed among seasons, with the lowest values and variation occurring during the summer and fall. High-light zones in gaps associated with the latitude at Coweeta Hydrologic Lab (slightly north of gap center; see Canham et al., 1990)
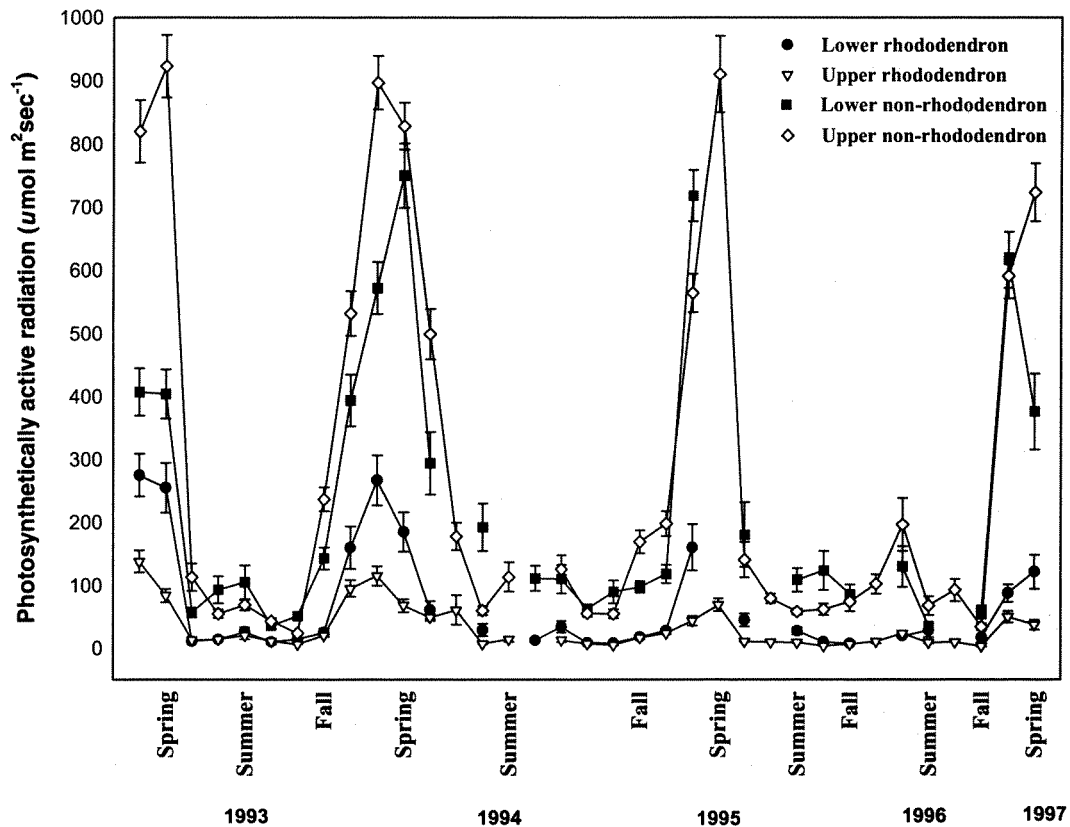
Fig. 1. Plot of photosynthetically active radiation (PAR; μmol m^2 s^{-1}) across 4 years of data collection for rhododendron and non-rhododendron gaps at two elevations. Notation: LR, lower elevation rhododendron; HR, high elevation rhododendron; L, lower elevation non-rhododendron; H, high elevation non-rhododendron. Individual points represent means within gap types ($N = 33$ for non-rhododendron gaps, $N = 11$ for rhododendron gaps). Error bars represent one standard error.

were apparent during the summer for non-rhododendron gaps at both elevations, and showed a similar pattern in non-rhododendron gaps at low elevation only during the spring. During the spring we observed a distinct high-light zone south of gap center in high elevation non-rhododendron gaps. This may have been a result of direct beam radiation penetrating the canopy through a nearby natural gap, which only occurred at low sun angles during that time of the year. A similar but less pronounced pattern occurred during the winter at the high elevation non-rhododendron and low elevation rhododendron gap. In rhododendron gaps, only a slight increase in PAR was detected on the north side of gap center during the summer at the low elevations. Changes in sun angle, heterogeneity in canopy structure, species-specific differences in phenology, and

the timing of senescence may account for the seasonal variation observed here.

There were substantial differences in PAR values when comparing seasonal means between gap and control on rhododendron and non-rhododendron sites (Table 1), but statistically significant effects of gap creation only occurred during the spring ($P = 0.014$) and summer ($P = 0.0014$) (Table 2). However, there was a significant rhododendron effect throughout the year (Table 2), and a significant interaction between rhododendron and gap creation occurred during the summer ($P = 0.02$). This suggests that although low seasonal mean PAR values were observed on sites occupied by rhododendron (Table 1), canopy removal on those sites significantly increased light levels. However, the magnitude of the increase, although statistically significant, is small
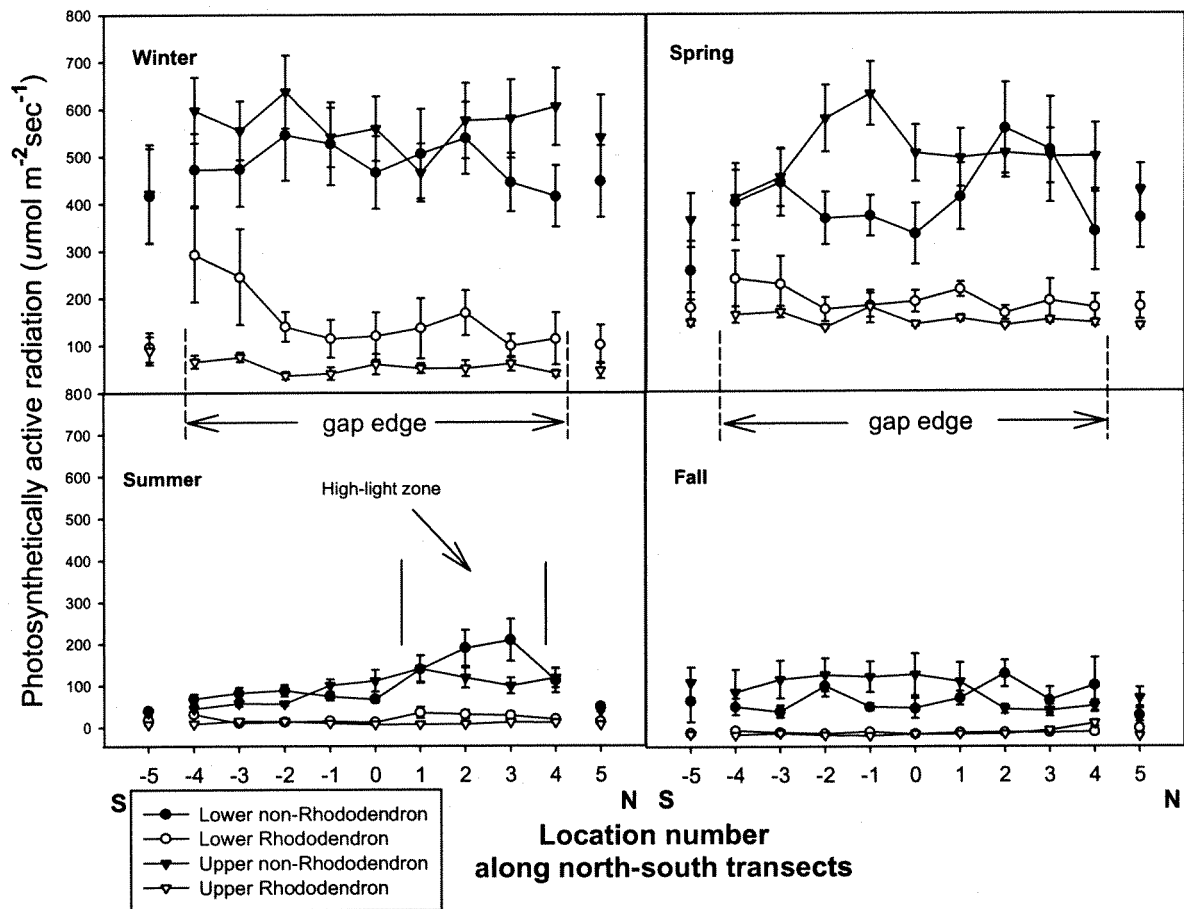
Fig. 2. Seasonal patterns of photosynthetically active radiation (PAR; µmol m^2 s^{-1}) for rhododendron and non-rhododendron gaps at two elevations. Individual points represent means within gap types ($N = 33$ for non-rhododendron gaps, $N = 11$ for rhododendron gaps. Error bars represent one standard error. Note: distance between locations 4 and 5 is approximately 10 m. Distance between all other locations is 2 m.

and perhaps represents little if any biological significance. PAR at 1 m during the growing season is roughly 10% of observed values during the dormant season. At this latitude (35°N), any potential increase in growing season light levels within gaps of the size examined here is partially neutralized by tree height (~25–30 m), canopy depth (15 m) and relatively high leaf area index (LAI; 4.3–5.4 m^2 m^{-2}) (Vose et al., 1995) especially in gaps with rhododendron understories where LAI commonly doubles that associated with the overstory.

Beckage et al. (2000) show only slight increases in the recruitment of new seedlings in small gaps, and the increases that were observed were due to heavier than normal seed production. Their study implies that the

coincidence of canopy removal and stochastically driven heavy seed production provides the most likely scenario for seedling recruitment following the death of individual canopy trees. It also suggests that only those species that are both intermediately tolerant to shade and exhibit large variation in inter-annual seed production are favored by this disturbance regime. Even though light is not required for seed germination in most species, adequate levels of PAR are needed for maintenance and continued growth once the photosynthetic apparatus develops. The amount of light required for maintenance varies among species. In a study of light compensation in two important southern Appalachian species Semones (1999) found that for naturally occurring seedlings of northern red oak

Table 1
Mean photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) and percent volumetric soil water content (%WC) by season of year and elevation[a]

Season	Rhododendron	Treatment	Photosynthetically active radiation (μmol m^{-2} s^{-1})		Volumetric soil water content (%)	
			Low elevation	High elevation	Low elevation	High elevation
Winter	Present	No-gap	99.5	67.9	39.7	36.9
	Present	Gap	135.9	47.9	24.1	38.6
	Absent	No-gap	432.2	480.9	33.9	33.1
	Absent	Gap	516.8	555.6	34.3	40.0
Spring	Present	No-gap	84.5	30.8	34.3	35.0
	Present	Gap	93.8	41.6	27.1	34.1
	Absent	No-gap	281.2	401.5	28.4	29.8
	Absent	Gap	422.4	620.2	29.5	36.4
Summer	Present	No-gap	15.4	7.1	32.5	38.9
	Present	Gap	21.5	9.2	28.9	40.8
	Absent	No-gap	44.4	38.4	31.9	31.8
	Absent	Gap	111.5	105.5	33.4	41.3
Fall	Present	No-gap	17.0	6.5	35.9	40.6
	Present	Gap	11.4	7.4	29.9	40.2
	Absent	No-gap	69.9	117.0	32.4	33.9

[a] For all gaps, means are calculated for the center-most 12 m. For non-gaps, means are calculated from the control locations.

under a closed canopy, light compensation occurred at PAR levels as low as 2.8 μmol m^{-2} s^{-1}. Similar values were observed for black cherry, showing that even under low light conditions photosynthetic rates for these species may be adequate for maintenance, and that small canopy openings may permit a sufficient amount of light to reach the forest floor for certain species. However, the absence of seedlings observed by Beckage et al. (2000) suggest that seedling survival is dependent on multiple factors, in addition to light.

5.2. Soil water content

Percent volumetric soil water content (%WC) in the upper 15 cm of soil varied both temporally and spatially (Fig. 3). There was a substantial decrease in available soil water in 1993 when rainfall amounts

Table 2
Results (*P*-values) from split-plot ANOVA (SAS Institute Inc., 1994) for effects of elevation, rhododendron understory cover, and gap creation (treatment), and their interaction terms by season of year on photosynthetically active radiation (PAR) at 1 m above forest floor, and percent volumetric soil water content (%WC) at 15 cm soil depth[a]

Parameter		Main effects			Interaction terms		
		Elevation	Rhododendron	Treatment	E × R	R × T	E × T
PAR	Winter	n.s.[b]	0.0023↓ (47.76)	n.s			
	Spring	n.s.	0.002↓ (52.72)	0.014↑ (13.7)	0.066 (6.30)		
	Summer	n.s.	0.015↓ (16.57)	0.0014↑ (40.18)		0.02 (11.21)	
	Fall	n.s.	0.004↓ (37.36)	n.s			
%WC	Winter	n.s.	n.s.	n.s.			0.072 (5.20)
	Spring	n.s.	n.s.	n.s.		0.062 (5.74)	
	Summer	n.s	n.s.	n.s.			
	Fall	n.s.	n.s.	n.s.		0.08 (4.95)	

[a] Arrows represent the direction of influence by main effects. Values in parentheses are the respective *F*-statistics.
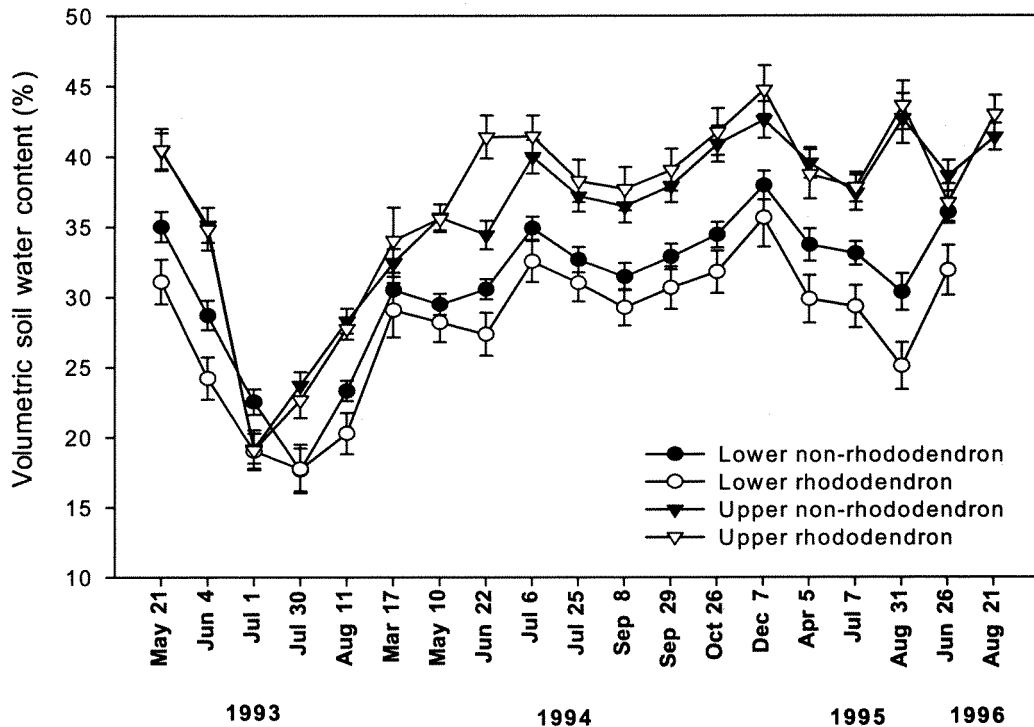[b] No statistical significance at the $\alpha = 0.10$ level.

Fig. 3. Plot of percent volumetric soil water content (%WC) across 3 years of data collection for rhododendron and non-rhododendron gaps at two elevations. Notation: LR, lower elevation rhododendron; HR, high elevation rhododendron; L, lower elevation non-rhododendron; H, high elevation non-rhododendron. Individual points represent means within gap types ($N = 33$ for non-rhododendron gaps, $N = 11$ for rhododendron gaps). Error bars represent one standard error.

within the Coweeta Basin were approximately 20% below the long-term mean. There was consistently lower %WC at the lower elevation site. We observed the highest levels of %WC in rhododendron gaps at the high elevation site and in non-rhododendron gaps at the low elevation site. During the summer, %WC showed the least amount of variability (Fig. 4). Overall, it was difficult to discern a pattern in %WC on a seasonal basis; however, during the summer and to a lesser extent the spring, %WC was slightly elevated around gap center at the high elevation site for both understory conditions, and somewhat less in the fall. Slightly elevated %WC at those gap center locations could be due to the lack of canopy interception of rainfall within the gap. When comparing gap versus control locations for rhododendron and non-rhododendron sites (Table 1) the trend is somewhat less consistent. Although there were substantial differences in the seasonal means, there was no statistically significant effect of elevation, rhododendron,

or gap creation on %WC (Table 2). However, an interaction between rhododendron and gap creation during the spring and fall ($P = 0.062$ and $P = 0.08$, respectively) suggests that there may be some effect on %WC by gap creation on sites occupied by rhododendron. The anomalous consistent drop in %WC at location -2 at both the lower and upper rhododendron gaps (Fig. 4) is due to the TDR rods being installed at a particularly droughty spot along the transect (e.g., high in organic material) and not to gap formation.

The differences we observed in soil moisture between gap and control represent small and likely biologically insignificant variation. Soil moisture is generally not limiting in this region under normal conditions, and differences of three to four percent (7.5% at the high elevation site) do not represent significant enough variation between treatment and control to elicit or inhibit a seedling recruitment response. Therefore, it is unlikely that these observed
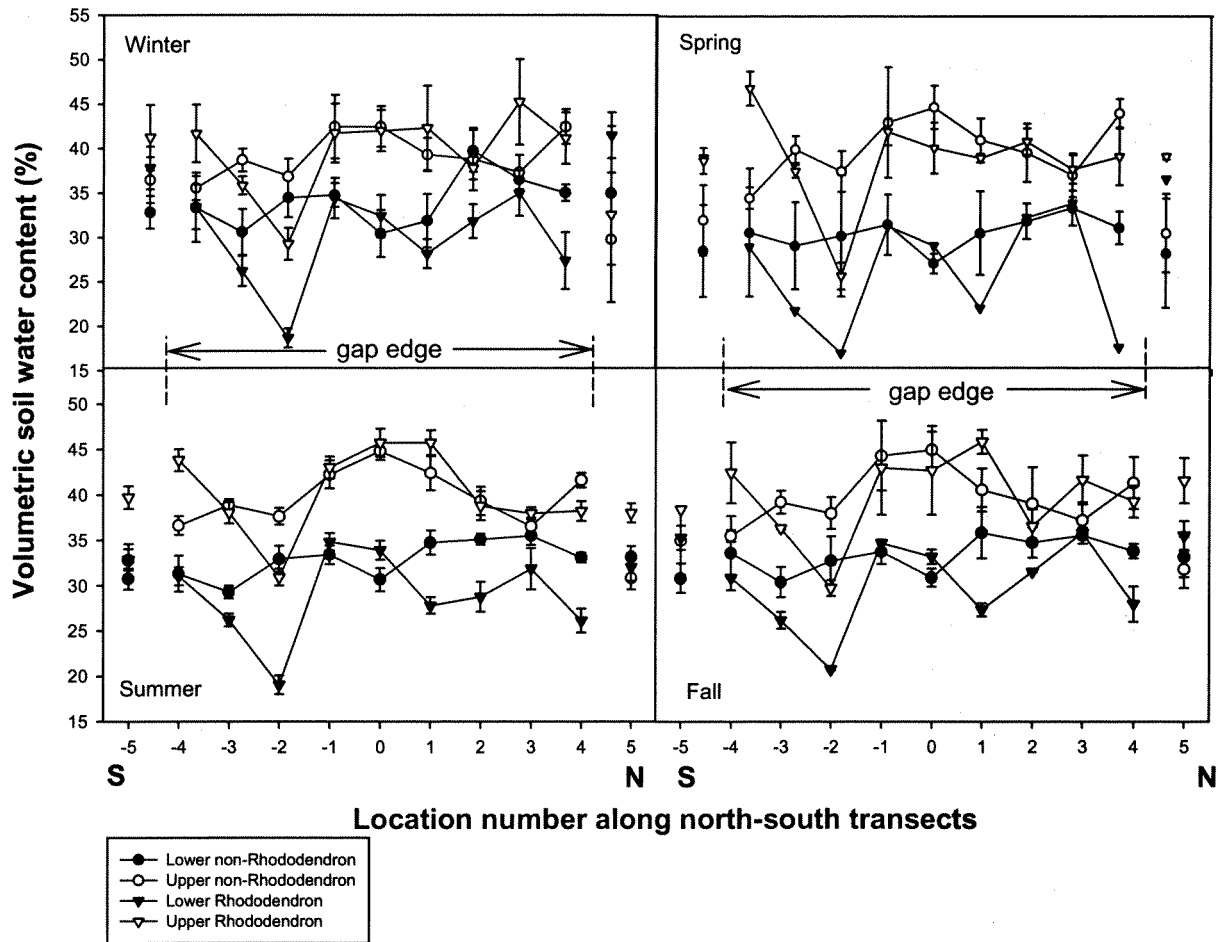

Fig. 4. Seasonal patterns of % volumetric soil water content (%WC) for rhododendron and non-rhododendron gaps at two elevations. Individual points represent means within gap types ($N = 33$ for non-rhododendron gaps, $N = 11$ for rhododendron gaps). Error bars represent one standard error. Note: distance between locations 4 and 5 is approximately 10 m. Distance between all other locations is 2 m.

differences are meaningful from the standpoint of canopy tree replacement.

5.3. Soil and air temperature

Considerable variation was observed in mean, maximum, and minimum soil and air temperatures between treatments and the presence or absence of rhododendron (Table 3a and b). However, we found no statistically significant effect of gap creation on mean, maximum, or minimum soil or air temperature during any season of the year (Table 4). There were, however, elevation and rhododendron effects related to soil and air temperature at various times through the year. During the spring mean, maximum, and minimum soil

temperatures were significantly less at the upper elevation site, and the presence of rhododendron further moderated mean and maximum soil temperatures (Table 4). In addition, there was a significant interaction effect between elevation and the presence of rhododendron on maximum and minimum soil temperature.

During the summer, mean and maximum air and soil temperatures were significantly lower at the high elevation site. Minimum soil temperature was also lower during the summer where rhododendron was present. As observed in the spring, there was an interaction between elevation and rhododendron leading us to conclude that the influence of rhododendron on minimum soil temperature varies with elevation. For the most part the significant effects we found were

Table 3

(a) Mean, maximum, and minimum soil temperature (°C) at 10 cm soil depth and (b) Mean, maximum, and minimum air temperature at 1 m above the forest floor by season, elevation, and treatment with and without rhododendron

Season	Elevation	Treatment	Rhododendron	Mean[a]	Maximum	Minimum
(a) Mean, maximum, and minimum soil temperature (°C) at 10 cm soil depth						
Winter	Low	No-gap	Absent	6.97 (0.044)	30.20	−2.77
		No-gap	Present	6.44 (0.058)	14.45	−5.96
		Gap	Absent	6.59 (0.046)	30.00	−3.17
		Gap	Present	6.58 (0.050)	14.52	−0.80
	High	No-gap	Absent	6.37 (0.030)	15.90	0.07
		No-gap	Present	6.21 (0.038)	11.89	−1.50
		Gap	Absent	6.20 (0.026)	14.38	−0.19
		Gap	Present	6.16 (0.035)	11.45	1.54
Spring	Low	No-gap	Absent	14.38 (0.059)	32.50	4.99
		No-gap	Present	13.92 (0.069)	18.07	7.85
		Gap	Absent	14.85 (0.055)	31.28	4.83
		Gap	Present	13.67 (0.067)	17.78	8.07
	High	No-gap	Absent	12.58 (0.044)	27.50	−2.77
		No-gap	Present	11.73 (0.057)	22.60	−8.00
		Gap	Absent	13.14 (0.039)	29.17	3.38
		Gap	Present	11.10 (0.040)	16.05	−0.46
Summer	Low	No-gap	Absent	18.57 (0.018)	23.68	11.74
		No-gap	Present	18.23 (0.025)	22.45	12.35
		Gap	Absent	18.90 (0.017)	24.31	11.68
		Gap	Present	17.86 (0.023)	21.74	12.25
	High	No-gap	Absent	17.12 (0.018)	23.65	11.22
		No-gap	Present	16.81 (0.029)	24.29	11.71
		Gap	Absent	17.34 (0.016)	23.12	11.04
		Gap	Present	16.27 (0.032)	19.71	10.65
Fall	Low	No-gap	Absent	11.82 (0.051)	23.62	−4.93
		No-gap	Present	11.90 (0.060)	18.73	1.36
		Gap	Absent	11.40 (0.045)	23.05	−5.07
		Gap	Present	11.58 (0.061)	19.13	3.48
	High	No-gap	Absent	11.48 (0.045)	24.11	4.67
		No-gap	Present	11.28 (0.059)	17.14	4.27
		Gap	Absent	11.17 (0.038)	19.62	3.83
		Gap	Present	11.26 (0.056)	16.99	6.29
(b) Mean, maximum, and minimum air temperature at 1 m above the forest floor						
Winter	Low	No-gap	Absent	7.70 (0.090	27.17	−15.76
		No-gap	Present	7.85 (0.130)	24.62	−13.94
		Gap	Absent	7.09 (0.075)	27.06	−16.30
		Gap	Present	6.78 (0.107)	24.48	−15.93
	High	No-gap	Absent	4.84 (0.077)	25.27	−17.96
		No-gap	Present	6.01 (0.103)	22.91	−15.56
		Gap	Absent	5.08 (0.073)	25.85	−18.11
		Gap	Present	5.88 (0.103)	23.89	−15.50
Spring	Low	No-gap	Absent	15.26 (0.077)	31.43	3.26
		No-gap	Present	16.12 (0.147)	29.69	1.74
		Gap	Absent	15.81 (0.072)	33.30	3.02
		Gap	Present	16.01 (0.147)	29.49	1.61
	High	No-gap	Absent	14.36 (0.085)	28.10	−3.02
		No-gap	Present	14.50 (0.105)	27.12	−0.71
		Gap	Absent	14.52 (0.073)	29.86	−3.08
		Gap	Present	14.47 (0.106)	27.55	−0.73

Table 3 (*Continued*)

Season	Elevation	Treatment	Rhododendron	Mean[a]	Maximum	Minimum
Summer	Low	No-gap	Absent	19.93 (0.038)	33.23	7.89
		No-gap	Present	19.20 (0.049)	30.69	7.56
		Gap	Absent	20.00 (0.032)	34.24	7.60
		Gap	Present	19.15 (0.050)	30.49	7.38
	High	No-gap	Absent	17.89 (0.037)	27.08	7.74
		No-gap	Present	17.84 (0.057)	25.71	7.58
		Gap	Absent	18.03 (0.031)	29.71	7.66
		Gap	Present	17.67 (0.057)	25.83	7.31
Fall	Low	No-gap	Absent	11.17 (0.082)	26.40	−7.06
		No-gap	Present	10.87 (0.104)	22.74	−7.03
		Gap	Absent	11.05 (0.065)	24.62	−7.42
		Gap	Present	10.35 (0.109)	22.58	−7.06
	High	No-gap	Absent	9.59 (0.093)	25.12	−7.52
		No-gap	Present	9.59 (0.124)	21.36	−6.75
		Gap	Absent	9.73 (0.076)	24.66	−7.54
		Gap	Present	9.48 (0.124)	21.34	−6.72

[a] Values in parentheses are standard errors.

Table 4

Results (*P*-values) from the split-plot ANOVA (SAS Institute Inc., 1994) for effects of elevation, rhododendron understory cover, and gap creation (treatment) and their interaction terms on mean, maximum, and minimum soil and air temperature by season of year[a]

Season	Source	Temperature (°C)	Main effects			Interaction terms		
			Elevation	Rhododendron	Treatment	E × R	R × T	E × T
Winter	Soil	Mean	n.s.	n.s.	n.s.			
		Maximum	0.0003↓ (136.75)	0.0006↓ (96.17)	n.s.	0.0053 (30.48)		
		Minimum	n.s.	n.s.	n.s.			
	Air	Mean	0.056↓ (7.14)	n.s.	n.s.			
		Maximum	n.s.	n.s.	n.s.			
		Minimum	n.s.	n.s.	n.s.			
Spring	Soil	Mean	0.006↓ (29.15)	0.075↓ (5.73)	n.s.			
		Maximum	0.0005↓ (111.11)	0.0003↓ (148.30)	n.s.	0.043 (8.55)		
		Minimum	0.039↓ (9.12)	n.s.	n.s.	0.093 (4.84)		
Spring	Air	Mean	0.004↓ (35.5)	n.s.	n.s.			
		Maximum	n.s.	n.s.	n.s.			
		Minimum	0.004↓ (36.79)	0.018↓ (15.00)	n.s.			
Summer	Soil	Mean	0.0002↓ (174.06)	0.023↓ (12.94)	n.s.			
		Maximum	0.078↓ (24.40)	n.s.	n.s.		0.10 (2.82)	
		Minimum	n.s.	0.039↓ (9.10)	n.s	0.009 (22.96)		
	Air	Mean	<0.0001↓ (341.2)	0.016↓ (16.08)	n.s.			
		Maximum	0.002↓ (61.73)	0.054↓ (7.35)	n.s.			
		Minimum	n.s.	0.003↓ (39.04)	n.s.			
Fall	Soil	Mean	n.s.	n.s.	n.s.			
		Maximum	n.s.	0.024↓ (12.70)	n.s.			
		Minimum	0.001↓ (73.46)	0.007↑ (25.0)	n.s.			
	Air	Mean	0.021↓ (50.49)	n.s.	n.s.			
		Maximum	0.031↓ (10.73)	0.039↓ (9.12)	n.s.			
		Minimum	0.09↓ (5.07)	n.s.	n.s.			

[a] Arrows represent direction of influence by main effects. Values in parentheses are the respective *F*-statistics.

consistent with what we expected. For example, at the high elevation site, where temperature is expected to be cooler, mean, maximum, and minimum soil and air temperatures were generally lower (Table 3b). The same held true for the protection from direct solar radiation that we expected rhododendron would provide. Where the evergreen shrub was present, there tended to be more moderate temperatures (Table 3a and b).

The only treatment effect, with the exception of interaction terms detected in this study, occurred for PAR only during the spring and summer. The lack of a detectable treatment (gap creation) response for temperature and soil moisture suggests that small-scale disturbances of this type have a minimal impact on temperature-dependent forest floor processes. In the absence of a heavy mast year very low levels of seedling recruitment would be expected (Beckage et al., 2000). Although there is evidence in the literature suggesting that small opening sizes may be more advantageous than larger openings for the regeneration of certain species (Cochran, 1969), microclimatic behavior within small (<300 m^2) canopy openings is very similar to that beneath an intact canopy. For openings of the size examined here and the species involved, topography and evergreen understory appear to be the primary determinants of spatial heterogeneity in understory microclimate.

6. Conclusions

It is commonly assumed that frequent disturbances exert the greatest amount of influence on ecosystem processes. In many systems, this may be true; however, it may not be the frequency itself, but the magnitude of a particular disturbance that most influences pattern and process. This study illustrates the lack of a significant effect of an important source of disturbance in forest ecosystems; e.g., standing tree death on understory microclimate. Temperature, soil moisture, and especially light, have long been known to drive tree replacement processes and the lack of a significant response in those variables where loss to canopy trees has occurred impedes succession. Studies have shown that maintenance of plant species diversity in forest ecosystems is closely linked to canopy disturbance (Bormann and Likens, 1979; Brokaw and Scheiner, 1989; Pickett and White, 1985; Shugart, 1984; Whitmore, 1989), but

often requires a concomitant disturbance in the understory (Beckage et al., 2000) as is often the case with windthrow, and is especially true in forests with dense understories (Veblen, 1982; Yamamoto et al., 1995). Dense understory vegetation has the effect of neutralizing the potential increase in limiting resources following disturbance to the overstory as was the case in this study. The implications of this influence pose a formidable challenge to forest managers who are charged with the task of either control of the understory vegetation or abandonment of those areas with regard to timber production.

The importance of a particular disturbance event, such as the creation of small canopy gaps, cannot be based on visual perception alone, but more importantly from an ecosystem perspective, on the scale of the relationship between the process or organism in question and the event itself. In order to adequately assess the effects of disturbance on ecosystem processes, it is essential to maintain a perspective that allows for the consideration of multiple outcomes.

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